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Meta-analysis of Summer Roosting Characteristics of Two Species of Myotis Bats

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ABSTRACT.—We compared roost site characteristics of the Indiana bat (*Myotis sodalis*) and northern bat (*M. septentrionalis*), which form maternity colonies in cavities and beneath bark of dead (snags) and living trees in eastern North American forests. We used published data (n = 28 sources; n = 1145 roost trees) from studies completed where the distributions of the two species overlap and evaluated a suite of habitat features that might affect roost selection and interspecific competition between these two congeners. We found no differences between these species in average height of roost aboveground, density of snags in the vicinity of roosts, selection of live trees versus snags or relative elevation. Populations of northern bats were more likely to choose roosts in crevices or cavities (88.9%) than Indiana bats (30.0%; $P < 0.1$), and roosted in trees that averaged smaller in diameter (30.0 $\pm$ 5.4 cm) than trees selected by Indiana bats (41.4 $\pm$ 2.4 cm; $P < 0.1$). Northern bats demonstrated greater variability than Indiana bats in height of roosts aboveground and in stem diameter of roost trees. Existing data indicate northern bats exhibit greater plasticity in choice of summer roosts than Indiana bats, explaining, in part, why northern bats are more widely distributed and more common in forests of eastern North America than are Indiana bats.

INTRODUCTION

The Indiana bat (*Myotis sodalis*) and northern bat (*M. septentrionalis*) are syntopic species that form maternity colonies in dead and living trees during summer months in eastern North American forests (Harvey, 1999; Lacki and Schwierjohann, 2001; Gardner and Cook, 2002; Menzel, 2002; Britzke, 2003b). More widely distributed than the Indiana bat, the northern bat occurs in forested habitats throughout the entire distribution of the Indiana bat (Harvey, 1999). Foster and Kurta (1999) compared habitat use between individual populations of these species and hypothesized niche overlap was likely and competition for limited roosting space a possibility when these species occur in the same habitats. These species differ markedly in abundance, population status and conservation priority. The Indiana bat has been listed as federally endangered since 1967 and distribution-wide population sizes continue to remain well below historic levels (US Fish and Wildlife Service, 1999). In contrast, the northern bat is believed to be relatively common throughout much of its distribution forming maternity colonies in both pine and hardwood forests (Lacki and Schwierjohann, 2001; Menzel, 2002; Broders and Forbes, 2004; Perry and Thill, 2007). In this paper we review existing literature describing characteristics of roosting habitat of the Indiana bat and northern bat. We evaluate these data in the context of possible interspecific competition for available roosting space between these species during the summer maternity season.

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METHODS

We surveyed published literature for data sets that described characteristics of summer roosting sites of Indiana bats and northern bats. We emphasized primary literature in our search, but also included gray literature sources that were known to us. We selected six habitat characteristics for comparison, emphasizing features associated with roost trees for which, at least, some data exist. These variables included roost tree diameter (cm), height of roost aboveground (m), density of snags in vicinity of roost trees (no. snags/ha), location of roost on the roost tree (beneath bark vs. inside a crevice or cavity), whether the roost was in a live or dead tree and relative elevation (lower elevation vs. higher elevation).

Within species and studies we distinguished data sets unique to sex and reproductive class combinations; hereafter, referred to as populations. We considered volant young with adult females (Mixed ♀), or adult males (Mixed ♂), as distinct populations because data for volant young were never published separately from adults by any author. We generated grand means (±SE) by species across populations for roost tree diameter, height of roost aboveground and density of snags in the vicinity of roost trees. For the latter character, when data were published on a per plot basis we converted values to numbers per hectare if sufficient information was available. Further, when variance in a data set was presented as standard deviation, values were converted to standard error (SE). Data for roost tree diameter, height of roost aboveground and snag density were tested between species with nonparametric Wilcoxon Two-sample Tests. To evaluate structures used for roosting on trees, live trees versus snags and relative elevation, we calculated % of populations where classes within roost characteristic (*e.g.*, live vs. snag) were shown to be associated with roost choice by bats. Within roost characteristic, assignment to classes was not mutually exclusive as populations of bats often demonstrated use of both groupings; thus, sums of percentages in almost all cases exceeded 100%. We used Chi-square Tests of Independence to evaluate relative importance of classes within roost characteristic to selection of roosts by these species. We used nonparametric tests to compare patterns of roost choice between species because number of roosts sampled in each population of inference varied and selection of roosts within populations was not independent. Thus, we could not assume normality of data for any population used in this analysis. All data were considered significant at $P \leq 0.1$.

RESULTS

We identified 28 published studies with data for at least one or more of the habitat characteristics evaluated, and where data were collected from populations located within overlapping distributions of the species. Data for Indiana bats represented one or more populations in 12 states including Missouri, Illinois, Indiana, Kentucky, Tennessee, Ohio, Pennsylvania, Virginia, North Carolina, Michigan, New York and Vermont. Data for northern bats represented one or more populations in seven states including Arkansas, Illinois, Indiana, Kentucky, Michigan, West Virginia and New Hampshire. Two additional studies on northern bats were from populations outside of the distribution of the Indiana bat and these data were not included in the analyses.

Total number of roosts represented in studies we compared was 915 for Indiana bats and 230 for northern bats, respectively (Tables 1 and 2). Average number of roosts per population was 38.1 ± 11.7(SE) for Indiana bats and 23.0 ± 4.8 for northern bats. Few studies presented data for males separately ($n = 4$), so direct comparisons of roost choice between females and males either within or between species were not possible.

Average roost tree diameter was 41.4 ± 2.4 cm and ranged from 62.0 to 20.0 cm for Indiana bats, and averaged 30.0 ± 5.4 cm and ranged from 65.0 to 12.7 cm for northern

TABLE 1.—A review of studies describing characteristics of summer roosting sites of Indiana bats (*Myotis sodalis*)

Source	Population of inference	Location	No. roosts (n)	Roost tree diameter (cm)		Roost height (m)		Roost location (bark vs. crevice)	Snag density (no./ha)	
				Mean	SE	Mean	SE		Mean	SE
Belwood (2002)	Mixed ♀	Ohio	2	37.8	(2.2)	7.5	(2.5)	(bark)	n/a	
Britzke (2003a)	Mixed ♀	New York, Vermont	31	46.0	—	n/a		n/a	n/a	
Britzke (2003b)	Mixed ♀	North Carolina, Tennessee	8	49.0	(9.2)	n/a		(bark)	83.3*	(83.3)
									50.0	(27.4)
Britzke (2006)	Mixed ♀	New York, Vermont	39	45.6	(4.0)	n/a		(both)	n/a	
Butchkoski and Hassinger	Adult ♂	Pennsylvania	2	20.0	(6.0)	8.5	(1.5)	(bark)	n/a	
(2002)	Adult ♀	Pennsylvania	5	28.4	(3.4)	8.0	(1.3)	(bark)	n/a	
Callahan (1997)	Mixed ♀	Missouri	54	58.4	(4.5)	n/a		(bark)	n/a	
Carter and Feldhamer (2005)	Adult ♀	Illinois	49	39.0	(2.0)	10.0	(0.8)	(bark)	n/a	
Gardner (1988)	Mixed ♀ & ♂	Illinois	26	32.3	(2.6)	n/a		n/a	n/a	
Gardner (1990)	Mixed ♀ & ♂	Illinois	51	n/a		n/a		(bark)	n/a	
Garner and Gardner (1992)	Mixed ♀ & ♂	Illinois	34	40.0	(2.8)	n/a		n/a	n/a	
Gumbert (2002)	Mixed ♀ & ♂	Kentucky	280	30.3	—	n/a		(both)	n/a	
Hobson and Holland (1995)	Adult ♂	Virginia	1	61.0	—	8.0	—	(bark)	n/a	
Humphrey (1977)	Mixed ♀	Indiana	2	n/a		n/a		(both)	n/a	
Kiser and Elliott (1996)	Mixed ♀ & ♂	Kentucky	11	27.4	(5.7)	n/a		(both)	n/a	
Kurta (1993a)	Mixed ♀	Illinois	1	56.0	—	5.0	—	(crevice)	n/a	
Kurta (1993b)	Mixed ♀	Michigan	8	36.5	(2.4)	9.2	(1.4)	(bark)	n/a	
Kurta (1996)	Mixed ♀	Michigan	23	40.9	(1.2)	9.9	(0.9)	(bark)	n/a	
Kurta (2002)	Mixed ♀	Michigan	38	42.0	(4.0)	10.0	(1.0)	(both)	n/a	
Kurta and Rice (2002)	Mixed ♀	Michigan	69	41.0	(2.0)	10.0	(1.0)	(bark)	n/a	
MacGregor (1999)	Mixed ♂	Kentucky	102	30.8	—	n/a		(bark)	n/a**	
Watrous (2006)	Adult ♀	New York, Vermont	50	48.0	(2.9)	n/a		n/a	n/a	
Whitaker and Brack (2002)	Adult ♂	Indiana	12	38.0	(4.3)	n/a		(bark)	n/a	
	Mixed ♀	Iindiana	17	62.0	(4.6)	n/a		(bark)	n/a	
Total, Mean (SE), or %			**915**	**41.4**	**(2.4)**	**8.6**	**(0.5)**	**30.0% used crevices**	**66.6**	**(16.6)**

* Authors provided snag densities for primary and secondary roosts, respectively

** Although not quantified, the authors stated that stands subjected to shelterwood harvests with snag retention supported more use of roosts by Indiana bats than stands where snags were felled during harvest

TABLE 2.—A review of studies describing characteristics of summer roosting sites of northern bats (*Myotis septentrionalis*)

Source	Population of inference	Location	No. roosts (n)	Roost tree diameter (cm)		Roost height (m)		Roost location (bark vs. crevice)	Snag density (no./ha)	
				Mean	SE	Mean	SE		Mean	SE
Carter and Feldhamer (2005)	Adult ♀	Illinois	19	37.3	(4.7)	9.2	(1.4)	(both)	n/a	
Foster and Kurta (1999)	Mixed ♀	Michigan	32	65.0	(1.0)	10.7	(0.04)	(both)	n/a	
Lacki and Schwierjohann (2001)	Pregnant ♀	Kentucky	18	30.3	(3.8)	6.8	(0.8)	(both)	44.5	(0.4)
	Lactating ♀	Kentucky	23	20.9	(3.3)	3.7	(0.6)	(both)	37.0	(0.2)
	Post-lactating ♀	Kentucky	7	12.7	(2.4)	4.3	(0.8)	(both)	32.0	(0.3)
Menzel (2002)	Lactating ♀	West Virginia	12	29.2	(1.6)	10.8	(1.0)	(crevice)	n/a	
Mumford and Cope (1964)	Mixed ♀	Indiana	1	n/a		n/a		(bark)	n/a	
Perry and Thill (2007)	Adult ♂	Arkansas	43	15.0	(1.3)	4.9	(0.6)	(both)	n/a	
	Mixed ♀	Arkansas	49	18.7	(1.0)	5.2	(0.5)	(both)	n/a	
Sasse and Pekins (1996)	Mixed ♀	New Hampshire	26	40.9	(2.8)	n/a		n/a	n/a*	
Total, Mean (SE), or %			**230**	**30.0**	**(5.4)**	**6.95**	**(1.0)**	**88.9% used crevices**	**37.8**	**(3.6)**

* Snag basal area significantly higher on roost plots than random plots

bats (Tables 1 and 2). Roost tree diameter was greater for roosts of Indiana bats than for northern bats ($W = 93.0$; $P < 0.04$). Average height of roosts aboveground was 8.6 ± 0.5 m and ranged from 10.0 to 5.0 m for Indiana bats, and averaged 6.95 ± 1.0 m and ranged from 10.8 to 3.7 m for northern bats. We found no difference between Indiana bats and northern bats in average height of roosts aboveground ($W = 63.5$; $P > 0.1$). Average density of snags in the vicinity of roost trees of Indiana bats was 66.6 ± 16.6 snags/ha and in the vicinity of roost trees of northern bats was 37.8 ± 3.6 snags/ha. We found no difference between Indiana bats and northern bats in snag density in vicinity of roost trees ($W = 9.0$; $P > 0.1$).

Indiana bats roosted beneath bark in 95.0% of populations compared, and inside crevices or cavities in 30.0% of the populations. In contrast, northern bats roosted, both beneath bark and inside crevices or cavities, in 88.9% of the populations. Selection of roost location between Indiana bats and northern bats was different ($\chi^2 = 2.93$; $P < 0.1$). Indiana bats used live trees in 69.6% of the populations studied and used snags in 95.6% of the populations. Northern bats used live trees in 88.9% of the populations studied, with 100% of the populations using snags. There was no difference is use of live trees versus snags among populations of these two species ($\chi^2 = 0.12$; $P > 0.1$). Relative elevation of roost trees was difficult to assess as most studies only qualitatively addressed this measure, if at all. When possible, data were generated based on our interpretation of study area descriptions. Results showed that Indiana bats were slightly more likely to select roost trees at lower elevations (56.2%; $n = 16$ studies) than higher elevations (43.7%). Northern bats, in contrast, chose roost trees at higher elevations (62.5%; $n = 8$ studies) more often than lower elevations (37.5%), but data were not different ($\chi^2 = 0.75$; $P > 0.1$).

DISCUSSION

Because of similarities in choice of summer roosts, Foster and Kurta (1999) suggested Indiana bats and northern bats might share a common ecological niche and compete for roosting sites when occupying the same habitats, especially when availability of suitable roosts is limiting. Our analyses, which are based on a more comprehensive evaluation of available data for these species, indicate considerable overlap occurs in characteristics of roosts chosen by these species, but differences also exist. These differences likely permit Indiana bats and northern bats to co-exist in habitats where they share living and dead trees as a common resource. We found northern bats used crevices or cavities in trees for roosting to a far greater extent than did Indiana bats that used exfoliating bark almost exclusively. This finding is consistent with direct comparisons made between these species by use of paired populations (Foster and Kurta, 1999; Carter and Feldhamer, 2005). Moreover, two additional studies of northern bats, not included in our analyses because of geographic location (*i.e.*, South Dakota and New Brunswick), also report populations of female (Cryan, 2001) and male (Broders and Forbes, 2004) northern bats using crevices and cavities instead of exfoliating bark. Our survey also demonstrated northern bats roosted in trees that averaged smaller in diameter than those chosen by Indiana bats; however, the range in average diameter sizes across populations of northern bats exceeded that for Indiana bats. Furthermore, even though height of roosts aboveground did not differ between the species, northern bats demonstrated a wider range of roost heights than did Indiana bats. These data indicate that these two species partition available roosting resources, with northern bats exhibiting greater variation in choice of roosting sites than Indiana bats, especially with regard to location of roosts on trees, selection of roosts by tree size and height of roosts aboveground.

Published data on sympatric populations of these species have demonstrated that northern bats roost in living trees more frequently than Indiana bats (Foster and Kurta, 1999; Carter and Feldhamer, 2005). However, our analyses did not detect a difference at the population level regarding use of live trees versus snags, as the majority of populations for both species used both live and dead trees. This provides further evidence that northern bats exhibit greater plasticity in roosting behavior than Indiana bats.

Meta-analysis of patterns of roost choice recorded in the literature demonstrated no difference between these species in relative elevation of roosts. Studies demonstrate Indiana bats choose roosts lower in elevation and avoid upland habitats, especially at the northern end of the species range (Brack, 2002; Britzke, 2006), with the reverse observed in southern populations (Britzke, 2003b). Avoidance of both higher slope positions and roosts in cluttered micro-habitats, especially for populations of Indiana bats in cooler climates near the northern extremes of the summer distribution, is presumed important in maintaining higher temperatures inside roosts and ensuring rapid development of young during shorter growing seasons (Britzke, 2003b).

One variable we could not evaluate in this study was slope aspect, as only a single study reported these data and no preference for slope aspect was detected (Watrous, 2006). Position of roost trees by slope aspect is likely to be important as roosts on south-facing exposures should be associated with warmer, drier conditions that result in higher temperatures inside roosting sites. Use of suitable roost trees on south-facing slopes would be consistent with numerous studies which have documented the need for solar-exposure in selection of roost trees by Indiana bats (Kurta, 1993b, 1996; Whitaker and Brack, 2002; Britzke, 2003b, 2006). Clearly, more data are needed to determine whether these tree-roosting bats choose roost trees based on slope exposure.

The paucity of data on density of snags at roosting sites of both Indiana bats and northern bats was a surprising outcome of this literature review, especially given the frequency at which these data are collected in studies of tree-roosting bats in western North American forests (Lacki and Baker, 2003; Kalcounis-Rüppell, 2005). Regardless, it is likely that greater snag densities could offer more choices for roosting sites and be beneficial to these two species of *Myotis*, especially Indiana bats. We encourage the collection of these data in future studies of roost selection by these species.

Our review was based only on data collected from throughout overlapping distributions of the species, so we believe that inferences here truly represent habitat choices of these species where they coexist. Data for Indiana bats came from 41% of the states where the species is known to occur (Harvey, 1999), although many states not represented are those for which only records of hibernating populations exist (USFWS, 1999). Northern bats have been studied to a lesser degree, as data were available from only 22% of the states within the distribution of the species (Harvey, 1999). Further, other than populations of northern bats in Nova Scotia (Garroway and Broders, 2007) and New Brunswick (Broders and Forbes, 2004), very little is known about the roosting behavior of northern bats throughout Canada, the northern limits of the species range (Harvey, 1999).

It is unclear to what extent tree roosts are limiting to bats inhabiting forested environments (Crampton and Barclay, 1998; Kunz and Lumsden, 2003). One study in New Zealand demonstrated only 1.3% of trees in the forest possessed cavities suitable for use by colonies of long-tailed bats (*Chalinolobus tuberculatus*) (Sedgeley and O'Donnell, 1999). The authors concluded that roosts were plentiful and likely not limiting to bats. Other studies have demonstrated differences in roost characteristics among syntopic species of tree-roosting bats (Boonman, 2000; Lumsden, 2002), suggesting competition for limited roosting space does occur among bats in some forested habitats. Our findings suggest Indiana bats and northern bats, two species which are sympatric throughout much of their distributions, also demonstrate differences in selection of roosting sites in trees. To what extent these differences in roosting characteristics render one species more or less vulnerable to changes in forested habitats remains uncertain. However, our survey of the literature found northern bats exhibited greater overall flexibility in choice of roosts, using both crevices and exfoliating bark for roosting, selecting trees for roosting across a wider range of stem diameters and heights and possibly choosing living trees to a greater extent (Foster and Kurta, 1999; Carter and Feldhamer, 2005). We believe these patterns explain, in part, why northern bats are more widely distributed and more common in forests throughout their distribution than are Indiana bats.

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